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MADROÑO

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EVOLUTION OF THE GALIUM MULTIFLORUM COMPLEX IN WESTERN NORTH AMERICA

I. DIPLOIDS AND POLYPLOIDS IN THIS DIOECIOUS GROUP

FRIEDRICH EHRENDORFER

The *Galium multiflorum* complex comprises a group of races which are spottily distributed through the interior of western North America. They occupy, for the most part, dry and rocky talus slopes and cliffs, and they range from the *Larrea* desert zone to alpine timberline. Life forms change correspondingly from low xerophytic desert shrubs to reduced alpine hemicryptophytes. All members of this racial complex are dioecious and sexually reproducing. Their mostly rotate, yellowish or greenish flowers are insect pollinated. Long silky hairs on the fruits facilitate wind dispersal.

The *Galium multiflorum* complex belongs to the section *Lopho-Galium* K. Schum. of this rubiaceous genus. Circumscription, differentiation, and first detailed taxonomic treatment along classical lines have been worked out by Ehrendorfer (1956). Further contributions, including a somewhat changed taxonomical evaluation, have been published by Dempster (1959).

Within the frame of a broad scientific project aiming at an understanding of the main evolutionary features of this world-wide genus along comparative lines (for publications available so far, see Ehrendorfer 1958), work on the *Galium multiflorum* complex has been continued and expanded since 1959. This has been made possible by financial support from a Rockefeller grant and especially from National Science Foundation grant number 9825. Under the guidance and extremely stimulating cooperation of Professor G. L. Stebbins, the author carried out intensive research work in 1959; this included study of habitats and accompanying vegetation for nearly all of the chief divisions of the *G. multiflorum* complex, collection of transplant material and extensive population samples for statistical analyses, cytological research, and comparison of practically all herbarium material available. Later this project was joined and continued by Lauramay T. Dempster, whose help in various respects is gratefully acknowledged.

The present research on the *Galium multiflorum* complex aims at a reconstruction of its evolution in time and space as part of the general unfolding of the Great Basin flora and vegetation since the Tertiary and at the demonstration of the main evolutionary mechanisms involved. Results will be published in a series under the general heading of which this is the first contribution. The main questions dealt with here are: (a) basic evolutionary mechanisms as elucidated by cytological behaviour; and (b) distribution of diploids and polyploids within the complex.

MATERIALS AND METHODS

Populations of various races of the *Galium multiflorum* complex studied in the field were designated by collection numbers. The italicized numbers in the text refer to the field collection numbers of the author and his various co-workers. Further data on these collections will be found in the detailed list of collections below. Transplant material was obtained and grown in the greenhouse of the Genetics Department, University of California, Davis, and later also in Orinda, California. Cultivation over long periods seems difficult, however, as requirements are quite specialized as to soil, temperature, etc. Carnoy solution (5 parts of 95 per cent alcohol: 3 parts of chloroform: 1 part of concentrated acetic acid) was used for the fixation of young flower buds in the field and of fresh shoot apices from transplanted material. Fixations were stored in the refrigerator. Saturated aceto-carmin with iron was employed for staining: anther material was squashed after short and gentle heating in the stain, whereas vegetative tissues were boiled in aceto-carmin for two minutes. A Zeiss standard Series GFL microscope was used for cytological work, and the drawings were made with a camera lucida. Herbarium vouchers from plants with known chromosome number will be deposited in principal herbaria after conclusion of the present research project.

GENERAL CYTOLOGY

Mitosis, meiosis and pollen grain mitosis were studied in various races of the *Galium multiflorum* complex. As a main result the existence can be established of a polyploid series with diploids, tetraploids and a local hexaploid (see discussion), all having the base number $x=11$. Apart from determination of chromosome numbers some general cytological observations have been made.

The dioecious sex differentiation in the group led to the question as to whether sex chromosomes were cytologically recognizable. Mitoses of shoot apices from male and female plants of the diploid *G. hallii* were carefully compared. No obvious difference in number or shape of chromosomes could be detected. One has to consider, though, that with relatively small and not very clearly differentiated chromosomes (fig. 1a), minor differences could easily escape notice. In various diploid and polyploid races meioses in pollen mother cells were scrutinized in order to find heteromorphic bivalents of sex chromosomes, but without success. Cytological differentiation of males and females in the *G. multiflorum* complex, therefore, seems to be absent or cryptic.

Comparisons were made of mitoses from shoot apices of very distantly related diploids, like *G. hallii* and *G. hypotrichium* subsp. *tomentellum*, in order to find out whether structural differentiation of chromosome sets had occurred (fig. 1a, b). Results show that there is much similarity. Absolute size differences apparent from the figures 1a and 1b may be due to the developmental stage of the individual cells. In both races the chromosome set consists of: A) one pair of SAT-chromosomes,¹ B) one pair

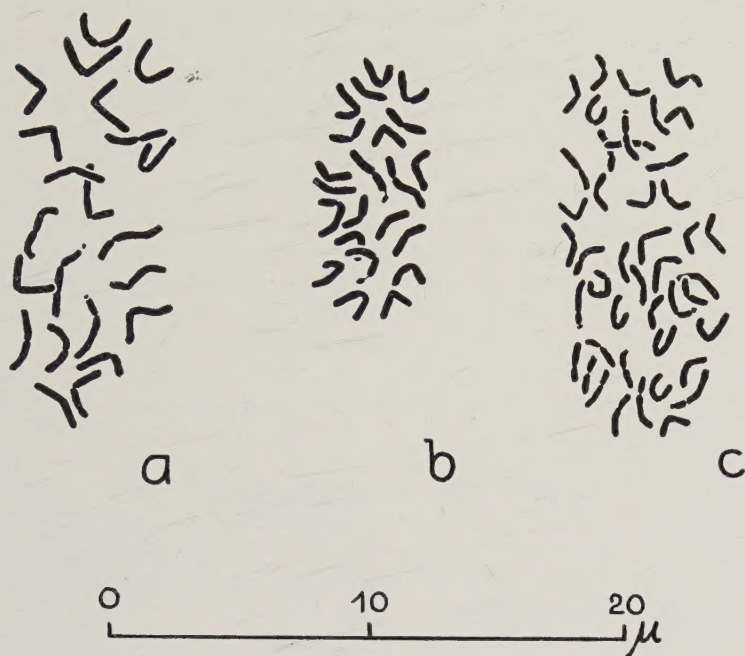


FIG. 1. Somatic mitosis in *Galium*. a, *G. hallii* (5901), b, *G. hypotrichium* subsp. *tomentellum* (5941), c, *G. grayanum* subsp. *glabrescens* (5963, tp. 2).

of long and strongly heterobrachial chromosomes, C) four pairs of chromosomes with less conspicuously different arms, and D) five pairs of chromosomes with median or submedian centromere. Groups C and D are not always clearly separable. This general pattern is also maintained in the allotetraploid *G. grayanum* subsp. *glabrescens* (fig. 1c). In spite of these similarities, indications for some structural differentiation can be found, e.g., in the SAT-chromosomes, where relation between long and short arms as well as satellite size are clearly different in *G. hallii* and *G. hypotrichium* subsp. *tomentellum*.

In spite of some cell-to-cell variability in chromosome size, there is a clear hereditary diminution of chromosome size with polyploidy. This is demonstrated better by comparison of somatic mitoses (fig. 1) from diploids than by comparison of corresponding stages of pollen meioses (fig. 2a, b) or pollen mitoses (fig. 2 l, m). Diminution of chromosome size is less obvious in the probably quite recent local hexaploid (fig. 2c). This reduction of chromosome size (and very likely nuclear size) in polyploids does not fully compensate the cell size increase correlated with

¹ The satellites often stick to the short arms, making it difficult to recognize the SAT-chromosomes. Such sticking seems to happen nearly always in pollen mitoses (fig. 2 l, m).

polyploidy, as is apparent from comparison of PMC's and young pollen grains which are larger in polyploids than in diploids (fig. 2a-c, l, m). Studies to determine the effect of polyploid level upon stomatal size are being carried on by Mrs. Dempster, with promising results for the use of stomatal measurement as an indication of ploidy when cytological evidence is lacking.

In polyploids of the *Galium multiflorum* complex there is occasional intra-individual somatic instability of chromosome number. This has been established for *G. grayanum* subsp. *glabrescens* (5963, tp. 1) and it probably occurs in *G. munzii* (5980, tp. c.). From excellent fixations resulting in exceptionally clear mitotic pictures, it is evident that the former plant has $2n=45$ as the most common number in young buds and shoot apices, but that occasional deviations occur, of which -44 -43 -42 -41 as a reductional series and -47 as an indication for accumulation were actually observed. One plant (5980, tp. c.) seems to vary between $2n=42$ -44 -45 . In a number of other polyploids, e.g., *G. grayanum* subsp. *glabrescens* (5963, tp. 2) and *G. munzii* var. *kingstonense* (5969), counts of numerous mitoses always gave the stable number $2n=44$. Intra-individual instability of chromosome number may be due to unbalanced primary number and/or spindle defects. Unstable somatic chromosome numbers have not been found in diploids.

Normal sexual reproduction is highly probable within the group. The course of pollen meiosis is remarkably normal in diploids and polyploids; male and female plants always coexist in the populations, often with an excess of males, and there is obvious morphological variability within the populations.

Chiasma frequency is variable. In the diploids with their relatively large chromosomes, frequency of bivalents with two chiasmata is often higher than 50 per cent, the other bivalents having only one chiasma (fig. 2d, e). Unpaired chromosomes seem to be extremely rare in the diploids. In the tetraploids with reduced chromosome size, the number of chiasmata is decidedly lower. In *G. hypotrichium* from Alpine County, for instance, there are only 15 per cent bivalents with two chiasmata in a plant from the Ebbetts Pass series (5920) and 10.9 per cent in a plant from the Sonora Pass series (5917) [each calculated from 50 PMC's]. Multivalents (trivalents with univalents and quadrivalents in chains and rings, fig. 2f) are relatively rare. In the above-mentioned plants there were 8 per cent PMC's with III+I and 28 per cent with IV (5920) and 8 per cent PMC's with III+I and 22 per cent with IV (5917). Univalents lag in anaphase I (fig. 2h), and are prematurely divided, but their halves are unable to divide a second time in anaphase II (fig. 2i); so they are eliminated or finally fuse with some of the telophase nuclei. As a result, pollen grains of polyploids occasionally contain deviating chromosome numbers (fig. 2m). This phenomenon must be basically responsible for some polymorphism of $2n$ numbers in populations of polyploids.

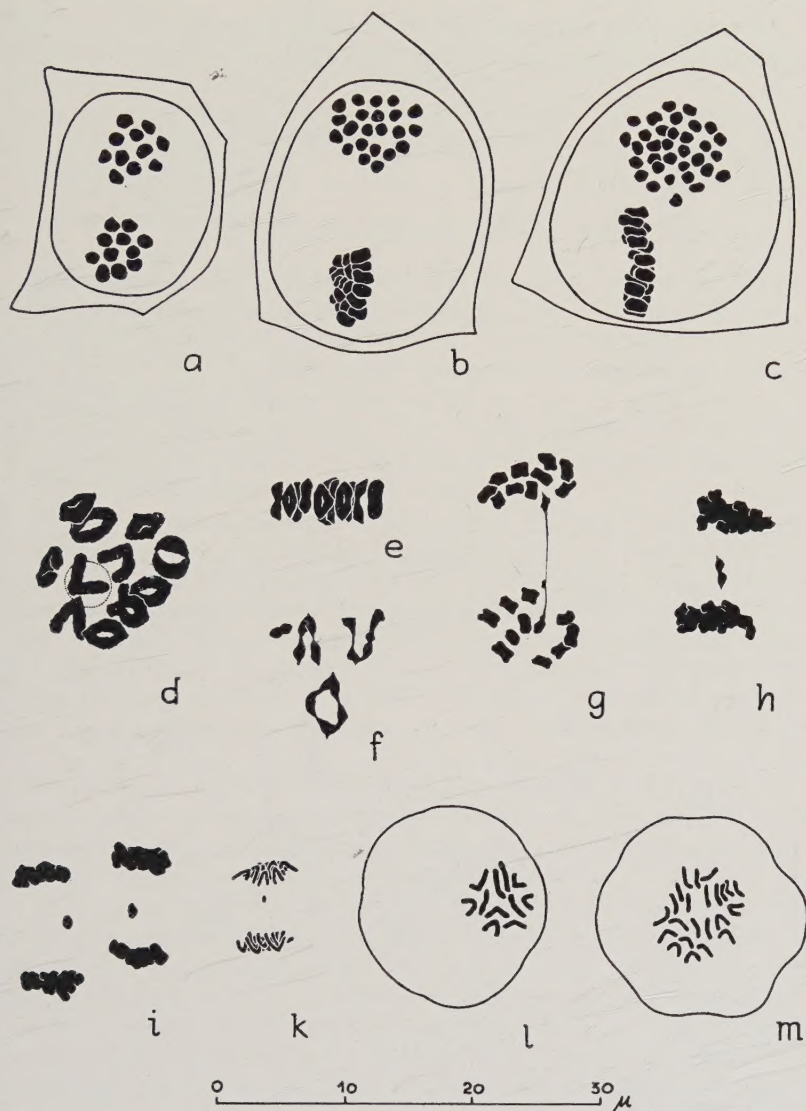


FIG. 2. Division figures in *Galium*. a-c, PMC metaphase II in diploid, tetraploid and hexaploid plants: a, *G. serpenticum*-2x (5911-5913, fd. IIa); b, *G. munzii*-4x (5903, tp.); c, *Galium* (6x race), Warner Mountains (5909, 5910). d-i, PMC divisions: d, diakinesis, *G. grayanum*-2x (5933-5936); e, metaphase I, side view, *G. serpenticum*-2x (5914); f, multivalents, III+I, IV chain, IV ring, *G. hypotrichium* subsp. *hypotrichium*-4x (5920); g, anaphase I with bridge and attached fragment, *G. parishii*-2x (5902); h, telophase I with lagging univalent, *G. hypotrichium* subsp. *hypotrichium*-4x (5917); i, telophase II with lagging univalent halves, *G. hypotrichium* subsp. *hypotrichium*-4x (5920). k-m, first pollen mitosis: k, anaphase with free acentric fragment, *G. hypotrichium* subsp. *hypotrichium*-2x (5916); l, metaphase *G. hypotrichium* subsp. *hypotrichium*-2x (5916); m, metaphase, aberrant pollen grain with $n=23$, *G. munzii* \times *G. hypotrichium* subsp. *subalpinum*-4x (5947).

In 3 diploids, 1 tetraploid and 1 hexaploid, consequences of chromosome aberrations have been seen: bridges with and without fragments in

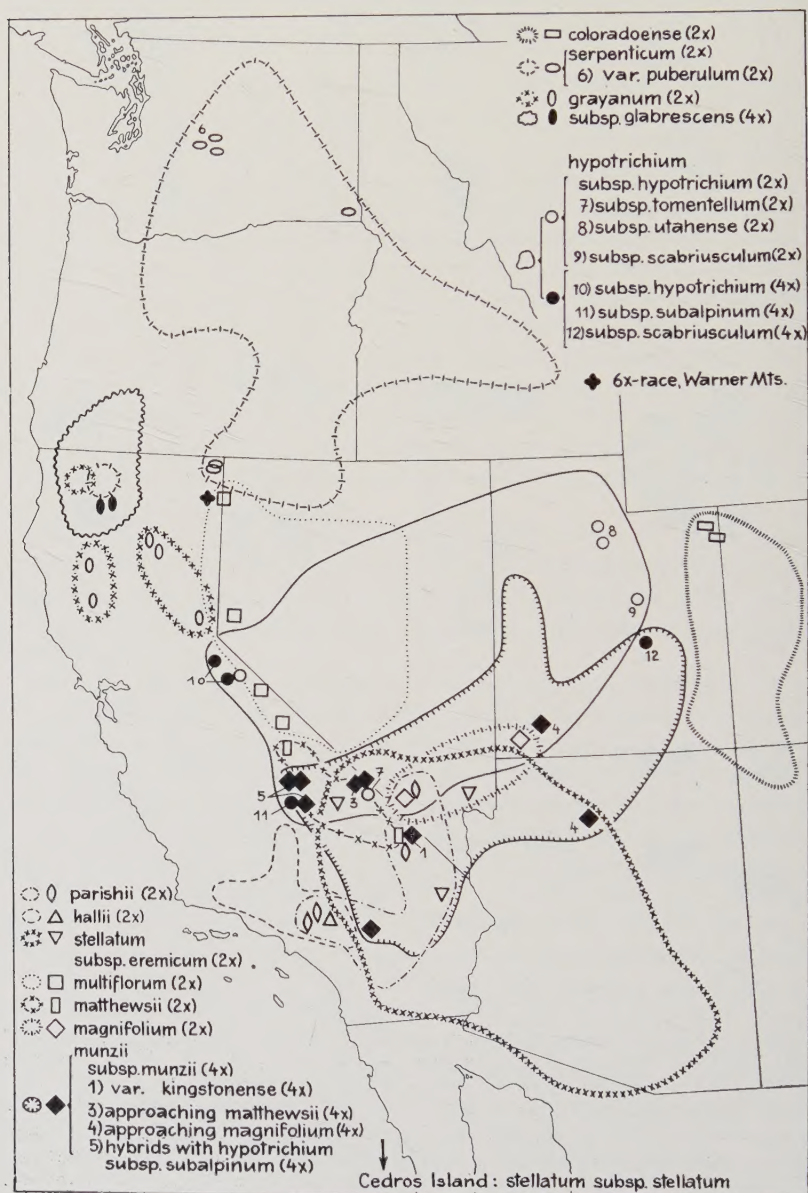


FIG. 3. Distribution of the *Galium multiflorum* complex, shown by outlines. Locations of populations examined cytologically are indicated by individual symbols.

anaphase I (fig. 2g), and liberation of attached fragments in anaphase of pollen mitosis (fig. 2k). In the hexaploid there are occasional spindle defects, restitution nuclei, and formation of resultant dyads.

Male sterility as a result of break-down of pollen development after normal meiosis has been observed in a diploid *G. serpenticum* plant from Mount Bidwell (5911).

DISTRIBUTION OF DIPLOIDS AND POLYPOIDS

Determination of chromosome numbers and ploidy levels is one of the major prerequisites for the reconstruction of the evolutionary history of the *Galium multiflorum* complex. So far, chromosome counts are available for most of the major species, subspecies, and hybrid populations presently recognized. These counts originate from 51 populations and more than 100 individuals. Populations with known chromosome numbers are shown on the map (fig. 3), as single symbols within the outlines of the total distributional area of their respective taxa.

The following list contains further information on geographical origin and habitat of the populations cytologically studied. The abbreviation "fd." indicates fixations made in the field, mostly comprising several individuals; chromosome counts in such instances usually refer to more than one individual. The abbreviation "tp." indicates fixations from single transplant individuals further designated by numbers or letters. Definite chromosome numbers are given after a minimum of several unquestionable counts per plant; if only one or few counts are available the symbol " \pm " is used. The abbreviation "ca." refers to approximate counts. Chromosome numbers are indicated in the diploid state ($2n$). They have been determined from vegetative tissues in flowers and shoot apices. Where counts have been carried out on pollen meiosis or pollen mitosis, $2n$ numbers have been extrapolated and an asterisk is added.

As is evident from the list, diploid populations are always uniform in respect to chromosome number ($2n=22$), while certain fluctuations of $2n$ numbers around straight x multiples have been observed in some polyploid populations: *G. munzii* from Wildrose Canyon ($2n=44, 46$), Lone Pine Creek ($2n=42, 44$), Zion National Park ($2n=44, 45$) and Grand Canyon ($2n=42, 44$). Polyploids are obviously less sensitive to aneuploidy, addition or loss of chromosomes, than diploids. The origin of aberrant types must be due to meiotic irregularities and deviating chromosome numbers in the gametes, or to intra-individual somatic instability, with similar consequences, situations which have already been referred to.

In the following list of collections, only previously published names have been used, and the taxonomic scheme followed is not necessarily in entire agreement with the author's present views. The taxonomic position of the plants in some of the populations represented is still uncertain, and their placement in the list is conservatively based on published work of the past.

GALIUM COLORADOENSE Wight

Utah, Dinosaur National Monument, 1 mile west of campground near Split Mountain, 5150 feet; Shinarump Quartz conglomerate; sandy and gravelly north slope, very open Pinyon-Juniper: *Ehrendorfer & Stutz 5950*. tp.: 2n=22

Utah, Uintah County, just south of Brush Creek on Highway 44, ca. 11 miles north northeast of Vernal, ca. 6000 feet; open bushy and herbaceous pioneer growth on steep Jurassic sandstone cliff: *Ehrendorfer & Stutz 5951*. tp.: 2n=22

GALIUM GRAYANUM Ehrendf.subsp. **GRAYANUM**

California, Tehama County, North Coast Ranges, South Yollo Bolly Mountain, 7700-8080 feet; gentle to steep talus slopes, metamorphic schists; subalpine pioneer vegetation among very open *Abies magnifica*: *Ehrendorfer 5933, 5934, 5935, 5936*. fd.: 2n=22*

California, Lake-Colusa County, Goat Mountain, North Coast Ranges, 6000 feet; leg. *G. L. Stebbins* fd.: 2n=22

California, Lassen National Park, Brokeoff Mountain, 9000 feet; gentle to steep talus slopes, volcanic andesite; subalpine pioneer vegetation: *Ehrendorfer, Stebbins & Dempster 5964, 5965, 5966, 5967*. tp. 0 : 2n=22
tp. 1 : 2n=22

California, Butte-Plumas County, Summit above Jonesville, ridge east of pass, 6700-7000 feet; rocks and talus slopes, volcanic andesite; pioneer vegetation among subalpine chaparral, *Abies magnifica* and *Pinus monticola*: type locality, *Ehrendorfer 5937, 5938, 5939*. fd.: 2n=22*

California, Placer County, Sierra Nevada, Sugar Bowl resort southwest of Donner Summit, 7200 feet; steep northeast slope, andesite talus and rocky outcrops; pioneer vegetation among *Quercus vaccinifolia*, *Abies magnifica* and *Pinus monticola*: *Ehrendorfer & Stebbins 5905*. fd.: 2n=22*

subsp. **GLABRESCENS** Ehrendf.

California, Siskiyou-Trinity County, west flank of Scott Mountain, ca. 6300 feet; ultrabasic intrusives; serpentine-peridotite; talus and gravel within very open *Pinus jeffreyi* and *Abies concolor*: *Ehrendorfer & Stebbins 5915*. fd.: 2n=44*

California, Siskiyou County, 0.5 mile south-southeast of Castle Lake, southwest of Mount Shasta village, ca. 6000 feet; serpentine talus, pioneer vegetation among *Arctostaphylos nevadensis*, *Pinus monticola*, *Abies magnifica*: type locality, *Ehrendorfer, Stebbins & Dempster 5963*.
tp. 1 : 2n=41-42-43-44-45-47
tp. 2 : 2n=44 (stable)

GALIUM HALLII Munz & Jtn.

California, Los Angeles County, northeast side of San Gabriel Mountains, Sawmill Canyon at west end of Swartout Valley, between Wrightwood and Lone Pine, 6600 feet; on steep north slopes, in mineral soil (schist) among *Quercus Kelloggii* and *Pinus ponderosa*: *Ehrendorfer 5901*. fd.: 2n=22

GALIUM HYPOTRICHIMUM Graysubsp. **HYPOTRICHIMUM**

California, Alpine-Mono County, Sierra Nevada, ca. 0.5 mile south of Sonora Pass, ca. 10,200 feet; wind-exposed talus slope on crest line, volcanic rocks; very scattered pioneers: type locality, *Ehrendorfer 5916*. fd.: 2n=22*
fd.: 2n=22

California, Alpine County, Sierra Nevada, ca. 2 miles west of Sonora Pass, ca. 9500 feet; sheltered west slope, volcanic talus; *Ribes* bushes and herbs: *Ehrendorfer 5917*. fd.: 2n=44*

California, Alpine County, Sierra Nevada, ca. 0.5 mile southeast of Ebbetts Pass, 8950 feet; northwest slope, volcanic talus; *Symphoricarpos*, *Artemisia*, herbs: *Ehrendorfer 5920*. fd.: 2n=44*

subsp. *SCABRIUSCULUM* Ehrendf. (*G. coloradoense* var. *scabriusculum* Dempster)
Utah, Carbon County, Castle Gate, side canyon on southwest of main valley, entrance ca. 1 mile northwest of the town, ca. 6500 feet; gully with steep sandstone slopes; grassy and herbaceous cover among open *Pinus ponderosa* and *Symphoricarpos*: Ehrendorfer & Stutz 5954. tp.: $2n=22$

Utah, Emery County, small side canyons on either side of Buckhorn Wash, ca. 1 mile north of San Rafael River bridge, ca. 4500 feet; dry bottom of gullies with boulders and sand from sandstone; very open Pinyon-Juniper and scrub: near type locality, Ehrendorfer & Stutz 5952, 5953. tp. a: $2n=44$

tp. b: $2n=\pm 44$

tp. c: $2n=\text{ca. } 44$

subsp. *SUBALPINUM* (Hilend & Howell) Ehrendf.

California, Inyo County, Sierra Nevada, Cottonwood Lake Basin, slopes north and northwest above Muir Lake, ca. 11,200 feet; granitic talus; open *Pinus balfouriana*, *Holodiscus* and pioneer herbs: Ehrendorfer 5945, 5946. tp. 1: $2n=\pm 44$

tp. 2: $2n=\pm 44$

subsp. *TOMENTELLUM* Ehrendf.

California, Inyo County, Panamint Mountains, Telescope Peak, below top on north side, ca. 11,000 feet; talus of metamorphic schists; pioneers among very open *Pinus aristata*: type locality, Ehrendorfer 5941. fd.: $2n=22$

subsp. *UTAHENSE* Ehrendf.

Utah, Utah County, Wasatch Mountains, American Fork Canyon, steep north slopes along trail to Timpanogos Cave, 6400–6800 feet; limestone rocks and talus; bushes and herbaceous pioneers among scattered *Pseudotsuga* and *Abies*: type locality, Ehrendorfer & Stutz 5949. tp.: $2n=22$

Utah, Salt Lake County, Wasatch Mountains, steep north slopes, ca. 1 mile southwest of Alta, ca. 9000 feet; limestone rocks and crevices; vegetation similar to 5949; Ehrendorfer & Stutz 5955. tp.: $2n=22$

GALIUM MAGNIFOLIUM (Dempster) Dempster

Nevada, Clark County, Charleston Mountains, southwest of Las Vegas, near Cottonwood Springs, canyon above Bar Nothing Ranch (= Wilson's Ranch), ca. 4200 feet; steep north slope along creek, alluvial material below mesozoic sandstone; open Pinyon with *Artemisia*, *Yucca* and *Opuntia*: type locality, Ehrendorfer & Dempster 5975. fd.: $2n=\pm 22$

tp.: $2n=22$

Utah, Washington County, ca. 1 mile northeast of Hurricane, steep slope above tributary of Virgin River, ca. 3000 feet; Jurassic sandstone and talus; with *Ephedra*, *Artemisia*, etc.; Ehrendorfer & Dempster 5979. fd.: $2n=22$

GALIUM MATTHEWSII Gray

California, Inyo County, east side of Sierra Nevada, Big Pine Creek, slopes above the camp site and road head, 8800 feet; loose granitic talus and sand, among *Artemisia*: Ehrendorfer 5922. fd.: $2n=22^*$

California, San Bernardino County, Kingston Mountains, steep slopes south of Kingston Pass, ca. 5500 feet; crevices of granite: Ehrendorfer & Dempster 5974. tp. a: $2n=22$

tp. b: $2n=22$

GALIUM MULTIFLORUM Kell.

California, Modoc County, south of Eagleville, cliff above Lower Alkali Lake, 5000 feet; in crevices and at the base of east-northeast-exposed basalt rocks: Ehrendorfer & Stebbins 5908. tp.: $2n=22$

California, Mono County, northwest shore of Mono Lake, on upper terrace, 6550 feet; among *Artemisia* and *Purshia* on light pumice sand: Ehrendorfer 5918. tp.: $2n=22$

Nevada, Storey County, Washoe Mountains, 2.2 miles north of Virginia City on Highway 17 to Reno, ca. 6600 feet; steep north slope, on volcanic talus among *Artemisia*, open Pinyon-Juniper along gully: type locality, *Ehrendorfer & Stebbins* 5906. fd.: $2n=22^*$

forma *HIRSUTUM* (A. Gray) Ehrendf.

California, Mono County, Sherwin Grade, dry wash southwest of Highway 6, ca. 6600 feet; volcanic rhyolite talus and rocks among *Artemisia*, open Pinyon: *Ehrendorfer & Dempster* 5921. tp.: $2n=22$

GALIUM MUNZII Hilend & Howell

var. *KINGSTONENSE* Dempster

California, San Bernardino County, Kingston Mountains, steep slopes south of Kingston Pass, in gullies and toward the top, 5800–6000 feet; rocky ravines and steep slopes with Pinyon, granite: type locality, *Ehrendorfer & Dempster* 5969, 5971.

tp. a: $2n=44$

tp. b: $2n=44$

subsp. *MUNZII*

California, Inyo County, Lone Pine Creek just above its break-through into Owens Valley, ca. 5000 feet; steep north slopes with Pinyon on granitic sand: *Ehrendorfer* 5927.

tp. a (glabrous form): $2n=42$

tp. b (hirsute form): $2n=44$

California, Inyo County, Panamint Mountains, Wildrose Canyon, above charcoal kilns, ca. 7200 feet; metamorphic schists and sandstones; open Pinyon and Juniper, talus: *Ehrendorfer & Dempster* 5968.

tp. a (hirsute form): $2n=44$

tp. b (hirsute form): $2n=44$

tp. c (glabrescent form): $2n=ca. 44$

tp. d (approaching *G. mathewsii*
= var. *carneum* Hilend & Howell, 1934): $2n=46$

California, Inyo County, Panamint Mountains, along trail from Mahogany Flat to Telescope Peak, ca. 8500 feet; metamorphic schists; talus, with *Holodiscus*, *Artemisia*, etc.: *Ehrendorfer* 5943. fd.: $2n=44^*$

California, San Bernardino County, San Bernardino Mountains, lower portion of Cushman Canyon, ca. 5000 feet; granitic talus, northeast slopes just above the wash, among open Pinyon-Juniper: *Ehrendorfer* 5903. fd.: $2n=\pm 44$

tp.: $2n=44^*$

probable hybrids with *G. HYPOTRICHUM* subsp. *SUBALPINUM*

California, Inyo County, east side of Sierra Nevada, Lone Pine Creek, 0.5 mile below Whitney Portal, steep ravine with northwest exposure, ca. 8370 feet; granitic boulders and talus; open *Chrysothamnus* and *Artemisia*: *Ehrendorfer* 5929. fd.: $2n=44^*$

tp.: $2n=\pm 44$

California, Inyo County, east side of Sierra Nevada, Little Cottonwood Creek above Lone Pine, ca. 8800 feet; granitic rock and sand; *Cercocarpus*, *Holodiscus* and *Artemisia*: *Ehrendorfer* 5947. fd.: $2n=44^*$

approaching *G. MAGNIFOLIUM*

Utah, Zion National Park, trail to The Narrows, ca. 4300 feet; sandy and gravelly talus below Navajo sandstone cliffs, eastern exposure; loose cover of herbs and scrub: *Ehrendorfer & Dempster* 5980.

tp. a (hirsute form): $2n=44$

tp. b (hirsute form): $2n=45$

tp. c (glabrous form): $2n=\pm 42-44-45$

Arizona, Grand Canyon National Park, south rim, uppermost portion of Grand View

Trail, ca. 7000 feet; arenaceous limestone; steep slope with herbs, among *Cercocarpus*, *Amelanchier* and *Pinus edulis* in northern exposure: *Ehrendorfer & Dempster 5981*.
 tp. a (somewhat hairy form): $2n=44$
 tp. b (glabrous form): $2n=42$

GALIUM PARISHII Hilend & Howell

California, San Bernardino County, San Bernardino Mountains, top of San Gorgonio Mountain, 11,485 feet: leg. *P. Raven 11,152*. fd.: $2n=22^*$

California, Los Angeles County, San Gabriel Mountains, hills about 2 miles north of Big Pines, ca. 6500 feet; granitic talus in northwest exposure: open *Artemisia* with *Pinus jeffreyi*: *Ehrendorfer & Grant 5902*. fd.: $2n=22^*$

California, San Bernardino County, Kingston Mountains, steep slopes south of Kingston Pass, ca. 5600 feet; granitic talus slopes and shady rock crevices: *Ehrendorfer & Dempster 5972, 5973*. fd.: $2n=22$
 tp.: $2n=22$

Nevada, Clark County, Charleston Mountains, Kyle Canyon, southwest slopes, southeast of Cathedral Rock camp site, ca. 7600 feet; limestone talus and rock crevices among open *Pinus*, *Abies* and *Cercocarpus*: *Ehrendorfer & Dempster 5976*.
 tp.: $2n=22$

GALIUM SERPENTICUM Dempster [*G. watsonii* (Gray) Heller sensu Ehrendf.]

Washington, Asotin County, Blue Mountains, below the crest overlooking Indian Tom Creek, 30 miles southwest of Asotin, ca. 5300 feet; basalt, rocks and fine talus below, open bushy and herbaceous pioneer growth: *Ehrendorfer & Ownbey 5956, 5957*.
 tp. 1: $2n=22$

California, Modoc County, Warner Mountains, Mount Bidwell, southeast side of plateau top, ca. 8000 feet; basalt talus; bushy and herbaceous pioneer vegetation with *Artemisia*, grasses, etc.: *Ehrendorfer & Stebbins 5911, 5912, 5913*.

tp. I: $2n=22$
 $2n=22^*$
 tp. II-1: $2n=22$
 fd. II: $2n=22^*$

California, Modoc County, Mount Bidwell, southwest side of plateau top, below rim, ca. 7600 feet; east slope, steep basaltic talus; similar vegetation: *Ehrendorfer & Stebbins 5914*. fd.: $2n=22^*$

var. **FUBERULUM** (Piper) Dempster [*G. watsonii* (Gray) Heller subsp. *puberulum* Ehrendf.]

Washington, Kittitas County, Wenatchee Mountains, west-southwest slope in upper Beverley Creek, ca. 4500 feet; serpentine rock and talus, open pioneer vegetation: *Ehrendorfer & Kruckeberg 5958, 5959*. fd.: $2n=22^*$
 tp. 1: $2n=22$

Washington, Kittitas County, Liberty, knoll above Boulder Creek, ca. 3500 feet; Eocene sandstone shale; sandy talus slope with pioneers: *Ehrendorfer & Kruckeberg 5960*. tp. 1: $2n=22$

Washington, Kittitas-Chelan County, south slope near Blewett Pass, ca. 4000 feet; sandy talus: *Ehrendorfer & Kruckeberg 5962*. tp. 1: $2n=22$

GALIUM STELLATUM Kell. subsp. **EREMICUM** (Hilend & Howell) Ehrendf.

California, Inyo County, Darwin Falls, about 3 miles south of Lone Pine-Death Valley highway, 3000 feet; rock crevices in canyon walls, metamorphic schists; desert scrub and some cacti: *Ehrendorfer & Dempster 5940*. fd.: $2n=22$

California, San Bernardino County, hills south of Highway 66, 7 miles northeast of Essex, ca. 1000 feet; steep rocky slope, gneiss; desert scrub (*Larrea*, etc.): *Ehrendorfer & Dempster 5982*. tp.: $2n=22$

Nevada, Clark County, Valley of Fire State Park, east entrance opposite Elephant Rock, ca. 2000 feet; rocky north slope, Triassic sandstone; desert scrub: *Ehrendorfer & Dempster* 5978. tp.: $2n=22$

UNNAMED TAXON (6x race)

California, Modoc County, Warner Mountains, Horse Mountain, south of and toward summit, ca. 8500 feet; basalt talus and rocks; grassy and shrubby pioneers: *Ehrendorfer & Stebbins* 5909, 5910. fd.: $2n=66^*$

GALIUM ROTHROCKII Gray subsp. *ROTHROCKII* (a monoecious member of section *Lopho-Galium*, not directly connected with the *G. multiflorum* complex).

Arizona, Grand Canyon National Park, south rim, uppermost portion of Grand View Trail, ca. 7000 feet; arenaceous limestone; steep slope with herbs, among *Cercocarpus*, *Amelanchier*, and *Pinus edulis* in northern exposure (together with *G. munzii* approaching *G. magnifolium*); *Ehrendorfer & Dempster* 5981A. tp.: $2n=22$

DISCUSSION

In spite of general dioecious sex differentiation, an eu-polyploid series $2x-4x-6x$ with $x=11$ has developed in the *Galium multiflorum* complex, just as in practically all of the hermaphrodite groups of this genus which have been checked cytologically so far. Polyploidization is less advanced than in some other groups with the majority of the races still diploid and only one very local hexaploid known. In the European section *Lepto-Galium*, for instance, polyploidization has proceeded to the $10x$ level, with the most widely spread and successful types (*G. pumilum*, *G. rubrum*, *G. marchandii*) on the $8x$ level (*Ehrendorfer* 1954).

Sexual differentiation in the *G. multiflorum* complex exemplifies an evolutionary trend established in a number of other New World groups of the genus as well. No sex chromosomes have been recognized so far. Sex differentiation in the complex must be similar in character to that in *Rumex* subgenus *Acetosella* or *Melandrium* (Löve and Sarkar 1956, and literature cited there). In these groups genetic sex determiners for the heterogametic sex are so strongly epistatic that polyploidization does not upset the 1:1 segregation mechanism ($XY = \sigma$, $XXXY = \sigma$, $XXXXXY = \sigma$).

The basic evolutionary differentiation of the *G. multiflorum* complex is accompanied by only very slight visible structural changes in chromosomes. Occasional spontaneous aberrations give a clue as to the origin of these.

As a result of the total evolutionary differentiation within this species complex, "marginal" and "extreme" positions in respect to distribution, ecology, and morphology are taken by diploids. Known sympatric contacts between diploids are rare. *Galium matthewsii* and *G. parishii* grow in mixed populations in the Kingston Mountains of southeastern California, but there are no indications of hybridization. This must be owing to the development of internal barriers, possibly involving chromosome structure. In contrast with the diploids, the polyploids are intermediate in distribution, ecology, and many morphological characters. There is some additional evidence that they are of hybrid origin and hybridize

much more freely with each other than do the diploids (e.g., *G. munzii* and *G. hypotrichium* subsp. *subalpinum* on the eastern slope of the southern Sierra Nevada). The present cytological findings substantiate the hypothetical racial diagram and interpretation developed by the author in 1956 (fig. 7): therein the polyploid *G. grayanum* subsp. *glabrescens*, *G. munzii*, and the partly polyploid *G. hypotrichium* form central "hot spots" of the complex, while all the marginal racial "cornerstones" are diploid. The general evolutionary situation therefore is very similar to that in other *Galium* groups, e.g. the section *Lepto-Galium* (Ehrendorfer 1954, 1955).

Details of cytological behaviour of the polyploid members of the *G. multiflorum* complex are very much in conformity with facts already known from European species: diminution of chromosome size in polyploid, stabilization of chromosome pairing, possibly via some influence on chiasma frequency, occasional irregularities of chromosome distribution into the gametes caused by formation of multi- and univalents and consequent appearance of biotypes with aberrant chromosome numbers. Intra-individual somatic instability of chromosome number has not been reported for *Galium* before, but the phenomenon seems not to be rare in polyploids (Gottschalk 1958, and literature cited there).

The cytological data here set forth point the way to some revisions in the taxonomic treatment of the *G. multiflorum* complex. The tetraploid *Galium grayanum* subsp. *glabrescens*, for example, should perhaps be accorded specific status, but in other cases specific separation on the basis of different ploidy levels seems impossible and highly impractical as within *G. hypotrichium* where even subspecific separation of the very closely adjacent and very similar $2x$ and $4x$ populations on Sonora Pass (Sierra Nevada) is an extreme procedure. Obviously no generalized rules can be applied in diploid-polyploid racial pairs, as has been previously shown with European *Lepto-Galium* and other groups. Taxonomic questions concerning the *Galium multiflorum* complex will be dealt with in other papers of this series.

SUMMARY

1. The western North American *Galium multiflorum* complex consists of sexual, dioecious races. Chromosome numbers have been established for most of the recognized taxa, including counts from 51 populations and more than 100 individuals. Primarily the chromosome numbers form an eu-ployploid series $2x-4x-6x$ with $x=11$. The distribution of the various diploids and polyploids is mapped.

2. Cell size (PMC's, pollen) is generally increased in polyploids.

3. Chromosome size and number of chiasmata are generally reduced in polyploids.

4. In two tetraploid plants a certain intra-individual somatic instability of chromosome number has been established; this has not been observed in diploids.

5. In polyploids there is a limited amount of multi- and univalent formation during PMC meiosis, with consequent irregularities of chromosome number in the gametes.

6. In four tetraploid (but never in diploid) populations, individuals with different standard chromosome numbers ($2n=42-44-45-46$) have been observed.

7. No differences in the chromosome sets of male and female plants could be demonstrated.

8. In PMC meioses and pollen mitoses some consequences of spontaneous chromosome aberrations (bridges, fragments) have been found.

9. Chromosome sets of various diploids and polyploids are quite similar, but there are certain differences (e.g. in the SAT-chromosomes) as a result of structural changes.

10. Cytological findings are briefly discussed from comparative evolutionary and taxonomic viewpoints.

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A NEW SPECIES OF *LYCIUM* IN NEVADA

CORNELIUS H. MULLER

A unique endemic *Lycium* occurs in Nevada in the area of the Atomic Energy Commission Nevada Test Site on Frenchman Flat. The plant was first discovered by Dr. William H. Rickard who remarked its extremely viscid, 4-merous corolla, and who suspected that it represented an undescribed species. It was collected in quantity by him, V. K. Carpenter, and Janice E. Beatley in the course of ecological investigations and subsequently by Dr. Beatley at my request. Material was submitted almost

simultaneously to C. L. Hitchcock and to me. Professor Hitchcock concurred in the opinion that the plant was undescribed and offered an analysis of its position in the genus but generously disclaimed any desire to undertake its publication. To him and to Dr. Beatley I am indebted for the opportunity to study this interesting material. Dr. Philip Wells has gathered considerable information on the distribution of the species. He discovered a large population on the southeasterly bajada of the Spotted Range and in northwestern Clark County. I am indebted to him for guidance to these localities.

The species typically grows on gravelly alluvium, predominantly limestone, in association with *Atriplex confertifolia* at the upper limit of *Larrea divaricata* and about the lower limit of *Coleogyne ramosissima*. It extends onto the playa clay on Frenchman Flat and onto quartzite beds on the lower slopes of the Spotted Range.

Lycium rickardii sp. nov. Frutex 0.5 m. altus, glaber; ramis albis spinosis; foliis 3–12 vel 18 mm. longis, 1.5–3 vel 6 mm. latis, 4–8-fasciculatis, obovatis vel spatulatis, floribus solitariis, pedicellis 0.5 mm. longis; calyce campanulato, tubo 6 mm. longo, lobis 4, 3 mm. longis; corolla tubuliformi, tubo 8–14 mm. longo, extra et intra viscido, lobis 4, circa 3 mm. longis; staminibus inclusis, corollae tubi partem supra mediam adhaerentibus, basi corollae intraque villosis; bacca subrotunda, 4–5 mm. longa, 2- vel 3-sperma, in calyce inclusa.

Intricately branched shrub about 0.5 m. tall or less; branchlets spinose, their smooth bark strikingly glaucous, weathering gray and fissuring after 2 or 3 years, the wood very soft and brittle; leaves 3 to 12 or even 18 mm. long, 1.5 to 3 or 6 mm. broad, in fascicles of 4 to 8, spatulate to obovate, the gradually narrowed base scarcely distinguishable from the blade, the apex broadly rounded, very thick and succulent, the midrib scarcely discernible in dried leaves, slightly glaucous green, the epidermal cells almost vesicular, giving the false impression of puberulence upon drying; flowers usually solitary in the leaf fascicles, the pedicels less than 1 mm. long; calyx highly variable, accrescent during and after anthesis, very succulent, the tube 6 mm. long, about 4 mm. broad, the 4 lobes 1 to 3 mm. long, mere teeth or broadly deltate-ovate, obtuse, broadly spreading or rarely erect; corolla white, the throat and veins suffused with purple or green, strictly tubular or narrowly funnel-shaped (the basal portion shrinking strongly upon drying), 8 to 14 mm. long, 2.5 to 3.5 mm. broad, the lobes about 3 mm. long, ovate, apically rounded, rotate or reflexed with age, 4-merous but a fifth lobe sometimes represented by a vascular bundle and an abortive petal, both outer and inner surfaces markedly viscid-glandular (this not apparent in dried material); stamens as many as the corolla lobes, an abortive petal sometimes carrying a full-sized staminode; filaments equal, plain, adnate about $\frac{3}{4}$ to $\frac{4}{5}$ the height of the tube, strikingly pubescent with long hairs in the basal $\frac{1}{3}$ or $\frac{1}{2}$ of their length; anthers included by the throat; gynoeceum bilocular, glabrous, with thin yellow walls, on a

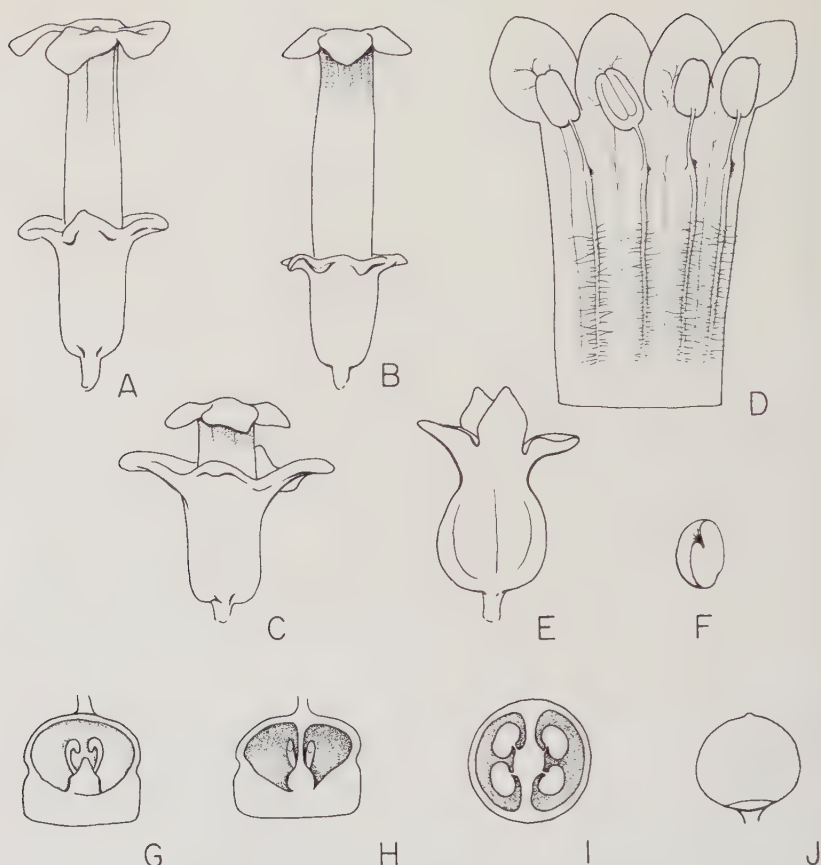


FIG. 1. *Lycium rickardii* sp. nov.: A-C, flowers, $\times 3$; D, interior of corolla, $\times 3$; E, fruiting calyx, $\times 3$; F, mature seed, $\times 3$; G, longitudinal section of ovary at anthesis parallel to the septum showing a pair of ovules on a single placenta, $\times 9$; H, longitudinal section of ovary at anthesis at right angles to the septum showing one of each pair of ovules on each placenta, $\times 9$; I, cross section of ovary, $\times 9$; J, mature fruit, $\times 3$. Drawn by Isabelle Haller from fresh material (Beatley 2, 3, 4 and Muller 10945) except in the instances of F and J which were based on Rickard and Beatley, 2 May 1959.

thickened bright red disc, each locule 2-ovulate, no abortive ovules and no lower cells developing in the disc; style at anthesis reaching about half the length of the corolla; stigma green, slightly 2-lobed, irregular; fruit subrotund, about 4 or 5 mm. long and broad, completely enclosed in the accrescent, urceolate calyx and surmounted by the constricted throat and divergent sepals, the exocarp cartilaginous, the disc remaining red and slightly fleshy but not enlarging with the fruit, 1 or 2 seeds maturing in each locule of the ovary, thus producing a 2-seeded or, more often, a 3-

seeded fruit, the seeds flattened on the common face, about 3 or 4 mm. long, minutely pitted, the aborted ovule(s) always in the original position.

NEVADA. Nye County: codominant in shadscale scrub at 4100 feet on south-facing bajada of the Spotted Range, 16.6 miles west of Indian Springs, 8 April 1961, *Muller* 10940, 10941, 10943, 10944, 10945 (holotype UCSB, sheet no. 8765), 10946, 10947; codominant in shadscale scrub at 4200 feet in southerly foothills of the Spotted Range, $\frac{1}{2}$ mile above the highway and 16.6 miles west of Indian Springs, 8 April 1961, *Muller* 10948, 10949, 10950; "east of playa" on Frenchman Flat, 2 May 1959, *Rickard* and *Beatley* s.n. (from which the fruit is described); "south of playa, near Lycium Plot 4;" "northwest of playa;" "near playa":¹ all on Frenchman Flat, 2 April 1959, *Rickard*, *Carpenter*, and *Beatley* s.n.; with *Larrea* and *Atriplex* south of playa at 3100 feet on Frenchman Flat, 11 April 1961, *Beatley* 2; with *Larrea* south of playa at 3100 feet on Frenchman Flat, 11 April 1961, *Beatley* 3; with *Larrea* east of playa at 3100 feet on Frenchman Flat, 11 April 1961, *Beatley* 4. Clark County: rare in shadscale scrub at edge of foothills $1\frac{1}{2}$ miles south of Indian Springs, 8 April 1961, *Muller* 10951.

All specimens cited are deposited in the herbarium of the University of California, Santa Barbara, and duplicates are being distributed.

Lycium rickardii negotiates Hitchcock's key (1932) past *L. pallidum* Miers (p. 202) but fits neither "G. Fruit 2-4-seeded, with 1 or 2 fertile seeds in the top of each carpel, and abortive ovules in compartment below" nor "GG. Fruit not as above, with more than four seeds." Rather, each locule contains two ovules, and there is no division of the locule into compartments as in *L. macrodon* and *L. puberulum*. If one ovule aborts, it appears on the same placenta and in the same locule with the matured seed. In this respect *L. rickardii* agrees with *L. shockleyi* Gray, an emended description of which was published by Muller (1940). The Hitchcock (1932) key may be emended as follows:

G. Fruit 2-4 seeded.

H. Fruit with each carpel divided into two locules, the upper bearing 1 or 2 seeds and the lower locule bearing aborted ovules; calyx not enclosing fruit.

L. macrodon and *L. puberulum*

HH. Fruit with one locule to each carpel, the seeds or abortive ovules totalling 2 in each locule; calyx enclosing fruit.

I. Fruit with an irregular suture or fold on one or both sides, filaments adnate nearly full length, the anthers appearing almost sessile. . . . *L. shockleyi*

II. Fruit lacking a suture or fold, filaments free in upper $\frac{1}{4}$ of $\frac{1}{5}$ of their lengths *L. rickardii*

GG. Fruit with more than 4 seeds. *L. cooperi* et seq.

The relationship of *L. rickardii* to *L. shockleyi* is apparent in the number of ovules in each carpel, the lack of a lower compartment with abortive ovules, and the 4-merous condition. However, the partially free filaments and lack of a suture or fold on the side of the fruit clearly distinguish it from *L. shockleyi*. Its fruit and stamen characters suggest *L. californicum* Nutt. ex Gray, but in the latter species the corolla is much smaller with proportionately shorter lobes and each locule contains a

¹ The latter two collections bear the following notes: "Corollas 4-merous, shining viscid within and without; shrub less than 2 feet high."

single ovule. Professor Hitchcock (personal letter to William H. Rickard, 22 November 1960) pointed out the intermediacy of *L. rickardii* between *L. californicum* and "such species as *L. macrodon* and *L. puberulum*." It might be added that both *L. rickardii* and *L. shockleyi* stand in this position with *L. rickardii* closer to *L. californicum* and *L. shockleyi* more similar to *L. macrodon* Gray, *L. puberulum* Gray, and *L. cooperi* Gray.

It is extremely likely that *L. rickardii* is somewhat more widely distributed than at present known. In the rather copious material at hand there is no evidence that heavy doses of irradiation at the Test Site are in any way responsible for the characters of *L. rickardii*. The longevity of these plants insures their being older than the Test Site, and their essential uniformity with those of the southerly and southeasterly range of the species makes it highly unlikely that the characters here noted might have arisen as a result of somatic mutation.

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SOME RECENT OBSERVATIONS ON PONDEROSA, JEFFREY AND WASHOE PINES IN NORTHEASTERN CALIFORNIA

JOHN R. HALLER

In an earlier paper (1959), I suggested that *Pinus jeffreyi* Grev. and Balf. is less susceptible to cold than is *P. ponderosa* Dougl. ex Lawson, and that for this reason *P. jeffreyi* replaces *P. ponderosa* at high altitudes in the mountains of California. Dr. Willis W. Wagener reported recently (1960), however, that established trees of *P. ponderosa* survived at least as well and occasionally better than *P. jeffreyi* following periods of severe cold in northeastern California. The purpose of the present paper is to present additional information on the pines of northeastern California which I believe will show that there is no discrepancy between Wagener's observations and my own, and that, in fact, they even reinforce one another.

In our respective papers, Dr. Wagener and I were discussing examples from different areas—his from northeastern California, mine mostly from cismontane California, that portion of the state lying to the west of the Sierra-Cascade crest. I deliberately omitted a discussion of the

northeastern Californian pines because the great bulk of the Ponderosa Pine in California occurs in the cismontane portion of the state, and because northeastern California is climatologically and floristically more closely related to the Great Basin region than to the rest of California. In addition, the ecological, genetic, and taxonomic relationships of the pines in northeastern California appear to be far more complex than in the remainder of the state. I am currently preparing a paper which will attempt to describe their relationships with each other and with the pines farther to the east.

There is considerable evidence available which supports the idea that *Pinus ponderosa* from cismontane California is more susceptible to low temperatures than either *P. jeffreyi* or *P. ponderosa* from more interior localities. The precise altitudinal zonation on the western slope of the Sierra Nevada, with *P. ponderosa* occupying the lower elevations and *P. jeffreyi* occupying the higher, is very suggestive of a difference in cold tolerance (Table 1). As I have indicated previously (1959), in the narrow zone where these species overlap, *P. jeffreyi* nearly always occupies the colder sites, such as canyon bottoms and the margins of low-lying meadows. Pearson (1931) reported that first-year seedlings of *P. ponderosa* from the Sierra National Forest (on the western slope of the Sierra Nevada) planted near Flagstaff, Arizona, were killed by a November freeze,¹ whereas seedlings from several other western states planted at the same locality were not injured. Weidman (1939) reported that young trees of *P. ponderosa* from the vicinity of Weed, California (west of the Cascade crest), planted near Sandpoint in northern Idaho were killed at the age of 12 years when the temperature fell rapidly from 45°F to -12°F. Trees of approximately the same age from 19 localities in Oregon, Washington, Idaho, Montana, South Dakota, Colorado, Utah, New Mexico and Arizona, planted in the same site as the Californian trees, survived the cold. Temperatures lower than -12°F occasionally occur within the range of *P. jeffreyi* in the western Sierra Nevada and within the range of both *P. ponderosa* and *P. jeffreyi* in transmontane northeastern California, but virtually never within the cismontane range of *P. ponderosa* (Table 1). The temperatures shown in Table 1 are the lowest that occurred in 1949, which was a year of record-breaking cold for many of the stations. This is the same year that Wagener observed fairly extensive damage to both *P. ponderosa* and *P. jeffreyi* in California. Table 1 shows that *P. ponderosa* occurs in the warmer cismontane localities and *P. jeffreyi* in the colder, but in transmontane California the two species grow in equally cold localities which are frequently colder than the coldest cismontane *P. jeffreyi* localities.

¹ Neither the temperature nor the year of its occurrence were given by Pearson. However, the coldest November temperature on record for Flagstaff for the years 1906-1930 is -4°F. This is probably not sufficiently cold to kill mature *P. ponderosa* from cismontane California (see Table 1), but was cold enough to be fatal to the more susceptible seedlings.

TABLE 1. MINIMUM TEMPERATURES IN 1949 IN CALIFORNIA.
Based on official records of the United States Weather Bureau*

A. Cismontane Localities

LOCALITY	COUNTY	ELEV.	TEMP.
Ponderosa Zone			
Placerville	Eldorado	1900 ft.	14° F
Sierra City	Sierra	4200	5°
Calaveras Grove	Calaveras	4800	5°
Yosemite Valley	Mariposa	4000	2°
Mt. Shasta (town)	Siskiyou	3500	1°
South Entrance, Yosemite N. P.	Mariposa	5100	-3°
Ponderosa-Jeffrey Zone			
Giant Forest	Tulare	6400	-4°
Grant Grove	Tulare	6700	-6°
Lake Spaulding	Nevada	5000	-8°
Jeffrey Zone			
Manzanita Lake	Shasta	5800	-3°
Huntington Lake	Fresno	7000	-10°
Twin Lakes	Alpine	7900	-24°
Soda Springs	Nevada	6700	-27°

B. Transmontane Localities

Ponderosa Zone			
Cedarville	Modoc	4700 ft.	-20° F
Mount Hebron	Siskiyou	4200	-22°
Alturas	Modoc	4300	-31°
Ponderosa-Jeffrey Zone			
Truckee	Nevada	6000	-19°
Sierraville	Sierra	5000	-25°
Boca	Nevada	5500	-41°
Jeffrey Zone			
Woodfords	Alpine	5600	-10°
Bridgeport	Mono	6400	-31°

* In some of the localities listed above, the species concerned does not occur in the immediate vicinity of the weather station. However, discrepancies between weather station temperatures and those in the adjacent pine localities have been kept to a minimum by selecting stations in situations that are ecologically similar to the pine localities and never more than a few miles removed from them. Stations have also been selected to show the maximum temperature variation within each zone.

The evidence given above indicates that *Pinus ponderosa* from north-eastern California is different physiologically from that on the cismontane slopes, since it survives temperatures lower than those that have killed cismontane *P. ponderosa* in experiments. This physiological difference is reflected in the relative distribution of *P. ponderosa* and *P. jeffreyi* in northeastern California, where these two species occur together over much more extensive areas than on the western slopes of the mountains. Furthermore, there is no tendency for *P. jeffreyi* to occupy the colder

sites within these extensive mixed stands, as occurs on the cismontane slopes.

In addition to the physiological—distributional differences between cis- and transmontane *Pinus ponderosa*, there are morphological differences. To begin with, the *P. ponderosa* from northeastern California is far more variable than that in the western Sierra Nevada, ranging from essentially identical to that farther west to something strikingly different. Because of this high variability, it is difficult to generalize about particular character differences. However, one character, needle thickness, shows relatively consistent differences between the west and east sides of the Sierra-Cascade crest. In all of the cismontane localities where I have measured needle thickness in mixed stands of *P. ponderosa* and *P. jeffreyi*, the mean thickness is greater in *P. jeffreyi*. In the typical examples given in Table 2A, the needles of *P. jeffreyi* average 0.19 mm. thicker than those of *P. ponderosa*, and the difference between the two species is highly significant at each of the three localities shown. Just the reverse is true on the east side of the Sierra-Cascade crest, where the needles of *P. ponderosa* average 0.12 mm. thicker than those of *P. jeffreyi* (Table 2B). However, east of the crest the differences between the species range from essentially nil at Sierraville to very pronounced at Hobart Mills. It is noteworthy that at Sierraville, where the needles of *P. ponderosa* are thinnest, the population is not unusually variable and is in most respects very similar to cismontane *P. ponderosa*. On the other hand, the *P. ponderosa* near Hobart Mills, which has much thicker needles than *P. jeffreyi*, is tremendously variable and for the most part very different from cismontane *P. ponderosa* (Haller, 1957). This thick-needled Hobart Mills population is located just three miles from Boca, which frequently has the lowest winter temperatures of any station in California (Table 1), suggesting that thick needles may be adaptively advantageous in cold climates.

There are at least three possible causes for the physiological and morphological differences between the cis- and transmontane *Pinus ponderosa* in northern California: environmental modification, differential selection from a heterozygous gene pool, and introgressive hybridization. A certain amount of environmental modification no doubt occurs in all populations of *P. ponderosa*, as the experiments of Weidman, the Institute of Forest Genetics, and my own observations (1957 and in press) have shown. However, these same experiments and observations show that the greater proportion of all physiological and morphological traits is genetically determined and cannot be ascribed solely to modification. Selection from a heterozygous gene pool has probably been the principal mechanism that has enabled *P. ponderosa* to occupy so many diverse habitats in western North America and to differentiate into a number of geographical races or subspecies. The geographical pattern of variation shown by these races is, however, a subtle one, and I have found that the

TABLE 2. MEAN NEEDLE THICKNESS IN PONDEROSA, JEFFREY AND WASHOE PINE POPULATIONS

A. Cismontane Localities

LOCALITY	COUNTY	ELEVATION (feet)	SAMPLE SIZE	MEAN NEEDLE WIDTH		SIGNIFI- CANCE OF DIFFERENCE
				PONDEROSA	JEFFREY	
Silver Fork, American River	Eldorado	6400	10	1.32 mm.	1.54 mm.	.004
Ebbetts Pass Highway	Calaveras	6300	24	1.60	1.75	.005
Shasta Valley	Siskiyou	4500	25	1.65	1.83	<.001
Mean of cismontane Ponderosa and Jeffrey populations:				1.52	1.71	

B. Transmontane Localities

Sierraville	Sierra	5000	25	1.78	1.78
Dixie Mtn. Game Refuge	Plumas	5700	10	2.01	1.88	.075
Hobart Mills	Nevada	5800	50	2.10	1.87	<.00003
Mean of transmontane Ponderosa and Jeffrey populations:				1.96	1.84	
				WASHOE	JEFFREY	
Mt. Rose, Nev.	Washoe	7200	25	2.05 mm.	1.88	.0006
Warner Mtns.	Modoc	7500	14	2.13	2.02*	.10
Mean of transmontane Washoe and Jeffrey populations:				2.09	1.95	

* The Warner Mountain Jeffrey Pine population is not sympatric with the Washoe Pine population, but is located a few miles away.

overall variability of the populations is usually about the same from one locality to the next. As already stated, many of the *P. ponderosa* populations in northeastern California differ strikingly from nearby populations and also display great variability. Such a pattern would be expected if hybridization were taking place.

The probable introgressant of *Pinus ponderosa* in northeastern California is *P. washoensis* Mason and Stockwell. One of the more outstanding characters of *P. washoensis* is its thick needles, which also characterize the variable *P. ponderosa* populations at Hobart Mills and Dixie Mountain Game Refuge (Table 2B). In addition there are other characters of *P. washoensis*, such as compact cones and short needles, which are prevalent in these variable *P. ponderosa* populations. I am still in the process of analyzing data from *P. ponderosa*, *P. washoensis*, and *P. jeffreyi* in northeastern California, but I am reasonably certain that the hybridization suggested here will be confirmed by further investigation.

The only published record of *Pinus washoensis* is from the type locality, on the watershed of Galena Creek, Mount Rose, Washoe County, Nevada (Mason and Stockwell, 1945). This locality is about 14 miles east of the Hobart Mills *P. ponderosa* population. A much more extensive

stand of *P. washoensis* occurs in the Warner Mountains, Modoc County, California. The best stands, which include many trees that are four feet in diameter, are located in the southern part of the range, in the general vicinity of the Patterson Ranger Station. Specimens from this area have been deposited in the herbarium of the University of California at Santa Barbara. Both the Mount Rose and Warner Mountain stands of *P. washoensis* occur above the 7000 foot elevation, apparently too high for *P. ponderosa*. The Mount Rose stand occurs sympatrically with *P. jeffreyi*, whereas the Warner Mountain stand occurs almost entirely above a narrow zone of *P. jeffreyi*. Additional stands of typical *P. washoensis* might well occur on other sufficiently high peaks in northeastern California. *Pinus washoensis* also occurs sporadically at lower elevations, for example in the variable "*P. ponderosa*" population near Hobart Mills. Very few individuals at this locality are "good" *P. washoensis*, but many of the trees in this apparent hybrid swarm are more similar to *P. washoensis* than they are to typical *P. ponderosa* (Haller, 1957).

The factors which limit the distribution of individuals of taxa such as *Pinus ponderosa*, *P. jeffreyi*, and *P. washoensis* are extremely difficult to circumscribe exactly. However, some idea of the relative cold susceptibilities of members of these taxa might be obtained from a series of experiments. For example, seeds of *P. ponderosa* and *P. jeffreyi* from the same site in the western Sierra Nevada and from northeastern California could be grown under uniform conditions, and the seedlings subjected to increasing intensities of cold. If a sufficient number of experiments were made, it would be apparent whether *P. ponderosa* is ever more susceptible to cold than *P. jeffreyi*, or if either or both species vary from one locality to another in their relative susceptibility. The results of any such experiments would have to be interpreted with caution, however. For example, *P. ponderosa* and *P. jeffreyi* from the same site in the western Sierra Nevada (near the upper altitudinal limit of the former and the lower limit of the latter) might be found to have an identical tolerance for cold. The upward migration of *P. ponderosa* could nonetheless be checked at this point by cold, because the species has exhausted its genetic potential for cold tolerance. *Pinus jeffreyi*, on the other hand, could have a much greater potential cold tolerance, which might be expressed only at higher altitudes, where it would be favored by natural selection.

The possibility also exists that the upward migration of *Pinus ponderosa* is not checked by low winter temperatures, but by insufficiently high temperatures during the growing season. Pearson (1931) stated that low summer temperatures are the principal deterrent to the success of *P. ponderosa* when it is planted at elevations above its normal range in the San Francisco Mountains of Arizona. In this region, *P. ponderosa* is limited to the valleys and lower slopes of the mountains where summer maximum temperatures are higher but winter minima are lower than in the Douglas Fir zone immediately above.

Evidence has been submitted in this paper that *Pinus ponderosa* from cismontane California is more susceptible to cold than is *P. jeffreyi*, that *P. ponderosa* from northeastern California is at least as tolerant of cold as is *P. jeffreyi* and that the spread of *P. ponderosa* to higher elevations is checked in Arizona by low summer temperatures rather than by extremes of cold in winter. Most of this evidence is indirect, and a more precise determination as to the factor or factors which limit *P. ponderosa* in its many different habitats will have to await the outcome of future experiments. For the present, it appears reasonable to postulate that low temperatures, whether in the form of low winter minima or low summer maxima, play an important role in limiting the distribution of *P. ponderosa*.

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INFLUENCE OF TEMPERATURE AND OTHER FACTORS ON CEANOTHUS MEGACARPUS SEED GERMINATION

ELMER BURTON HADLEY¹

One of the striking characteristics of chaparral is the absence of any kind of seedlings beneath mature, undisturbed stands. After such disturbances as bulldozing or fire, however, an abundance of seedlings appears, suggesting that scarification or heat make the germination possible (Cooper 1922, Went *et al.* 1952, Horton & Kraebel 1955, Quick 1959).

The density and dryness of this chaparral brush cover in California, the accumulation of large quantities of dry litter beneath the brush, and the Mediterranean type climate, all combine to create an extreme fire

¹ The author wishes to express his thanks to the University of California at Santa Barbara for extending the full use of its facilities and to Dr. L. C. Bliss and Dr. C. H. Muller for generous aid and advice in the course of this study.

hazard during the long summer droughts. Many chaparral species are so specifically adapted to the resulting periodic fires as to indicate a long history of subjection to recurrent fires in the geologic past (Jepson 1925). Horton (1945) found that *Ceanothus* species in general have a life span of about forty years. In areas unburned for a period of at least forty years, however, other species have, to a large extent, replaced *Ceanothus* because there has been no regeneration by *Ceanothus*.

Two fire responses are very common among chaparral species: resprouting from burls (underground root crowns) that are not killed by fire, and heat induced seed germination due to cracking of impervious seed coats. *Arctostaphylos glandulosa*² is an example of a species that shows the first type of fire response. Almost no seedlings of this "stump sprouting" species are found following fires. *Ceanothus megacarpus*, wherein the entire shrub is usually killed outright by fires, represents the second type of response—regeneration by seed following fire. Other shrubs, such as *Adenostoma fasciculatum*, exhibit both types of fire responses.

In addition to the resprouting shrubs and seedlings of chaparral species, a recently burned-over area contains many annuals and short-lived perennial herbs and subshrubs as well as weeds. Eventually the chaparral vegetation dominates and the under vegetation perishes.

Fire or heat induced increases in germination were first investigated by Wright (1931), who found that oven heating greatly increased the germination of a number of chaparral species, including *Ceanothus megacarpus*. Sampson (1944), and Went *et al.* (1952) have also investigated increased germination of chaparral species due to fire. Stone & Juhren (1951), investigating germination of seeds of *Rhus ovata*, found that temperatures of 80°C induced the rupturing of impervious seed coats and thus permitted water to reach the embryos. Quick (1935), using seeds of several species of *Ceanothus*, also found that heat cracked the impervious seed coats. Stratification, following the heat treatment, resulted in further germination increases in these species.

In none of these investigations, however, were the possible modifying effects of natural field conditions on heat induced germination considered. In the present investigation an attempt was made to determine the effect of temperature, of mechanical injury, and of accumulated litter on the germination of seed of *Ceanothus megacarpus*.

METHODS

Except for field observations and collecting the seeds, all other phases of this investigation were carried out in the greenhouse of the University of California at Santa Barbara. All results obtained must, therefore, be considered no more than suggestive of what might occur under field conditions.

² Nomenclature is that of Munz (1959).

Large quantities of *Ceanothus megacarpus* seeds were gathered from the Santa Ynez Mountains above Santa Barbara, California, in June, 1959, and air dried for two months in the laboratory. Voucher specimens are on deposit at the herbarium of the University of California at Santa Barbara.

All experiments were conducted in controlled temperature boxes, using sterilized petri dishes with moistened filter paper. All seeds were treated with the fungicide, Semesan. Seeds were germinated at a temperature regime of 26°C and 17°C (alternating 12-hour periods at each temperature). Each experiment was conducted for a thirty-day period, and germination in all cases was defined as emergence of the radicle.

In order to determine the effect of heating or cutting of the seed coat on *Ceanothus megacarpus* seed germination, a first experiment was run using three lots of seeds. The first lot was subjected to a temperature of 100°C for 5 minutes in an electric oven, the second to mechanical rupturing of the seed coat at the micropilar end with a razor blade, and the third lot served as controls (no heating or cutting). Each of the above three treatments consisted of three replicates using 25 seeds per dish. These seeds were moistened with distilled water and germinated as described in the previous paragraph.

In order to determine the possible effects of leaf litter on germination, a second series of experiments was set up using actual leaf material on top of the seeds in the petri dishes. Sets of seeds were prepared, each with three replicates as in the previous experiment, i.e., heated seeds, cut seeds, and controls. Fresh leaves, duff (dead fallen leaves not yet decayed beyond recognition), and ashed duff (7 grams of duff ashed at 700°C in a muffle furnace for 45 minutes) of *Adenostoma fasciculatum* were used in equal quantities on each of the first three sets of seeds, while a fourth set of three petri dishes of seeds was left as a control. *Adenostoma fasciculatum* was chosen because it is one of the most abundant and cosmopolitan species comprising the chaparral community. Except for the presence of leaf material, the seeds were germinated with distilled water as in the previous experiment. To test the hypothesis that any stimulation of seed germination due to duff is really a mineral effect, another part of this second experiment was run using a modified Hoagland's solution containing trace elements (Hoagland and Arnon 1950) in place of the distilled water.

In the third experiment, the effect of using leached duff (partial removal of minerals) was investigated. The duff was leached in eight changes of distilled water for 96 hours before being placed over the seeds.

All data were subjected to an analysis of variance using the individual degrees of freedom technique (Snedecor 1956). Space does not permit its inclusion, but a complete analysis of variance for the data may be found in Hadley (1960).

TABLE 1. EFFECT OF TEMPERATURE, MECHANICAL RUPTURING OF SEED COAT, AND *ADENOSTOMA FASCICULATUM* LEAF LITTER ON *CEANOTHUS MEGACARPUS* SEED GERMINATION.

Percentage Germination*		Cut seed	Heated seed (100° C for 5 min.)	Untreated seed
Treatment				
I.	Distilled water	86	23	0
II.	Distilled water +			
	<i>Adenostoma</i> duff	87	75	1
	<i>Adenostoma</i> duff ashed	41	24	0
	<i>Adenostoma</i> fresh leaves	24	13	0
	Control	83	25	0
	Hoaglands solution +			
	<i>Adenostoma</i> duff	95	57	0
	<i>Adenostoma</i> duff ashed	31	29	0
	<i>Adenostoma</i> fresh leaves	21	21	0
	Control	88	77	1
III.	Leached duff	85	41	1
	Unleached duff	87	80	4

* All experiments run in replicates of 3 with 25 seeds in each replicate.

Experiment I—Effect of heating and cutting of seed coat on *Ceanothus megacarpus* seed germination.

Experiment II—Influence of *Adenostoma fasciculatum* leaf litter and/or Hoagland's solution on the germination percentage of *Ceanothus megacarpus* seeds.

Experiment III—Effectiveness of leached *Adenostoma fasciculatum* duff vs. unleached duff in stimulating *C. megacarpus* seed germination.

RESULTS

Under the conditions of this investigation, germination of *Ceanothus megacarpus* seeds is facilitated by either heating or cutting the seed coats. As shown in Table 1, however, mechanical rupturing is the more effective treatment.

Presence of the various *Adenostoma* leaf material did not significantly affect the germination of the untreated controls, but did significantly affect the germination of the heated and cut seed (Table 1). Presence of duff over the heat treated seeds significantly stimulated the germination percentage of these seeds, resulting in a four-fold increase over the controls. This increase was shown by later experiments to be attributable to increased minerals made available by the decayed duff. Since cut seeds displayed maximum germination with or without duff being added, the effect of adding duff could not be measured accurately in the case of the cut seed.

Presence of fresh leaf material resulted in a significant reduction of cut seed germination, possibly due to the presence of an inhibitor in the fresh leaves (Naveh 1960). Application of ashed duff also caused a significant reduction in the germination of cut seed.

Substitution of Hoagland's solution in place of distilled water resulted in little change in the germination per cent of seed treated with

either ashed duff or fresh leaves (Table 1). These results show that fresh leaf material or ashed duff have the same inhibiting effect, whether distilled water or Hoagland's solution is used. Germination per cent of heated seeds is very similar, whether treated with distilled water plus *Adenostoma* duff or only with Hoagland's solution. Leaching of this duff (partial removal of minerals) significantly reduced the effectiveness of duff in stimulating germination of the heat treated seeds (Table 1).

DISCUSSION AND CONCLUSIONS

Ceanothus megacarpus seed germination percentage was increased by heating these seeds for 5 minutes at 100°C. Mechanical rupturing of the seed coat was found to have an effect similar to heating, but to a greater degree. This would suggest that the stimulatory effect of heating involved in this species is primarily one of rupturing a previously impervious seed coat, thus allowing water to reach the embryo. The smaller increases in germination in the case of the heated seed may be due to injury to some of the embryos due to heat, to a random cracking of the seed coat away from the micropilar end which might hamper radicle emergence, or to the variability in seed coat thickness (some of the seed coats may not be cracked by this particular temperature).

Application of leaf material of another chaparral species, *Adenostoma fasciculatum*, has a definite effect on the germination percentage of *Ceanothus megacarpus*. *Adenostoma* duff enhances the germination of heat treated *C. megacarpus* seeds. Since a similar effect was obtained when Hoagland's solution was substituted in place of the distilled water and duff, this stimulation of germination can possibly be attributed to increasing mineral concentration provided by the decaying duff. The conclusion that germination was stimulated by available minerals in the duff is supported by the fact that there was marked reduction in percentage of seed germination when the seeds were topped by leached duff.

The apparent inhibition of germination by fresh leaves of *Adenostoma* may be due to the presence of an inhibitor or inhibitor complex in these leaves (Naveh 1960). The reduced germination of cut seed in the presence of ashed duff may be due to increased pH. Sampson (1944), using several grass species, has noted this ash inhibition, which was attributed to increased pH. The germination percentage of heated seeds in the presence of ashed duff, remained similar to that of non-treated heated seeds. This would suggest that ashed duff did not have an inhibitory effect on heated seed.

What part heating, mechanical rupturing, and plant litter actually play in the field can only be suggested, for in the field the situation created in the laboratory does not exist. Obviously, rupturing of the seed coat due to mechanical injury can be of only minor ecological significance in the field except where bulldozing, sharp deer hoofs, or some other agent may crack the seed coats. Accidental rupturing may therefore account for at

least a portion of the few young seedlings that are sometimes found in disturbed but unburned areas.

The extremely low percentage of germination noted for untreated seed may serve to explain the field observation that young seedlings of *Ceanothus megacarpus* are not found under undisturbed, mature chaparral in which this species is a constituent. Heat treatment of *Ceanothus megacarpus* seeds by fires should be of tremendous importance in the repopulation of burned areas. This increase in germination percentage due to cracking of the seed coat by heat could account for the abundance of *Ceanothus* seedlings found immediately following a fire.

It must be remembered that all chaparral fires are not alike; they differ in intensity, duration, and temperatures reached during the fire. Some fires consume both shrub crowns and litter; others are principally confined to the shrub crowns leaving pockets of litter unconsumed. Therefore a differential destruction of duff by fire is noted in the field. Some fires could easily provide the required temperatures for the duration of time necessary to crack the seed coats and yet not burn away all of the duff that would be present. Other fires, even though they might burn away most or all of the duff and seeds, would still provide temperatures necessary to crack the seed coats of those seeds which were buried in and therefore protected by the soil. Thus breaking of the seed coat by heat would account for the *Ceanothus* seedlings that Quick (1959) and others have encountered after fires in the chaparral.

Only *Adenostoma fasciculatum* leaf litter was used in these experiments. It is possible that the duff and fresh leaves of many of the other chaparral species might exhibit similar effects on *Ceanothus megacarpus* seeds and those of several other chaparral species. This is a subject that would indeed be worth further investigation.

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REVIEWS

Flora of the Santa Cruz Mountains of California. A manual of the vascular plants. By John Hunter Thomas. viii + 434 pages, 249 figs. and 16 photos, 1 map. Stanford University Press, Stanford, California. 1961. \$8.50.

The first impression, upon taking up the "Flora of the Santa Cruz Mountains," is of an attractive, well-designed book with clear typography, generous spacing, indented keys, good illustrations, and with an adequate binding. The Stanford University Press is to be congratulated upon producing a volume of exceptionally fine appearance.

Although the book is entitled "Flora of the Santa Cruz Mountains," it encompasses the whole San Francisco peninsula, and thence southward to the Pajaro River and from the ocean east to the middle of the Santa Clara Valley. Coverage is comprehensive, including both native and introduced plants. The number of kinds of introduced plants occurring spontaneously is amazing; 31 per cent of the 1799 taxa listed fall into this category.

For each of the species listed, Thomas gives the scientific name, common name, habitat, localities in the area, time of blooming, and place of origin for introduced species. Sometimes elevation is given and, occasionally, associated species. Brief comments, often on taxonomic problems, are made for some species. Synonyms are included only for convenience in referring to the same taxon in other regional and sectional floras. Specimens are not cited except in a few instances. There are no new names or combinations.

The flora is written for the serious beginner as well as the trained botanist. The beginner, especially, will appreciate the 250 line drawings which are from the "Illustrated Flora of the Pacific States." As a result of better spacing and better paper they are clearer and more attractive than many of the original reproductions in the Illustrated Flora. The common names also appear to correspond to those used by Abrams. Possibly the influence of the latter flora may be responsible in part for the recognition of certain families, for example, Melanthaceae, Parnassiaceae, Hydrangeaceae, Grossulariaceae, Amygdalaceae, Malaceae, Mimosaceae, Caesalpinaceae, Monotropaceae, Pyrolaceae, Vacciniaceae, Convallariaceae, Amaryllidaceae, all of these segregated from the Liliaceae, Saxifragaceae, Rosaceae, Fabaceae, and Ericaceae. Nevertheless, Thomas' taxonomic concepts are, in general, conservative. For example, *Berberis* rather than *Mahonia* is recognized; *Montia exigua* is considered as synonymous with *M. spathulata*; ssp. *decurrens* of *Eriogonum nudum* is not recognized. However, *Dudleya* (not *Echeveria*) and *Horkelia* are used; *Allium breweri* is considered distinct from *A. falcifolium*; and all the forms of *Arctostaphylos* in the Santa Cruz Mountains are accorded specific status. The varietal designation is usually employed rather than the subspecific except when the latter designation has been used

in a recent monograph. The arrangement of families in general follows the sequence proposed by Engler and Prantl.

Part I consists of 33 pages of introductory material and 13 pages of keys to the divisions, classes, subclasses, and families. A map shows place names and supplements the description of the area. The geology (4 pages including a stratigraphic profile) is discussed by Dr. Earl E. Brabb. Monthly and yearly average temperatures and average rainfall are given for seven stations. Classification of the vegetation follows Munz and Keck insofar as it may be applied to the Santa Cruz Mountains. The more characteristic plants are listed for each of the plant communities, and photographs illustrate most of them.

Ten pages are devoted to a discussion of the composition and relationships of the flora. The number of native species is approximately 1246 in the Santa Cruz Mountain area of 1386 square miles, compared to 1004 in Marin County (529 square miles), 700 in the Mount Hamilton Range (1500 square miles), and 530 on Mount Diablo (55 square miles). Five distributional patterns are recognized, whereas Campbell and Wiggins recognized 16 for the whole state. Endemic in the area are 10 species, 3 subspecies, 11 varieties, 2 forms, and 1 hybrid. Some are closely restricted to certain geological formations.

Lists, together with localities, are given: 1) of taxa reaching their southern limits of distribution in the area, 2) of taxa reaching their northern limit, 3) of those with affinities with the inner Coast Ranges, 4) of the more obligate serpentine taxa, and 5) of plants with a disjunct distribution to the north. Plants of sandhills and marshes are also discussed. The list of taxa with "their northern limits of distribution in the Coast Range in the Santa Cruz Mountains" applies to the "Outer Coast Ranges" only, as seven species are included which occur somewhat farther north in the Inner Coast Range, on Mount Diablo. These are *Anemopsis californica*, *Malacothamnus hallii* (*Sphaeralcea fasciculata*), *Osmorrhiza brachypoda*, *Linanthus ambiguus*, *Pholistoma membranaceum*, and *Salvia mellifera*.

Of the 34 taxa occurring in the Santa Cruz Mountains, but regarded by Thomas as being typically species of the Inner Coast Ranges, 24 grow in the Mount Hamilton Range. Only 19 are on Mount Diablo, 13 of which are common to Mount Diablo and the Mount Hamilton Range. Whether *Helianthella castanea* should be considered a plant of the inner ranges is debatable.

Thomas' list of "the more obligate local serpentine plants" (p. 31) caused the writer considerable surprise, as a number of plants which are common and widespread on Mount Diablo are included. The following species are not associated in the writer's mind with serpentine although the records indicate that they may, at times, grow on serpentine: *Festuca pacifica*, *F. reflexa*, *Koeleria macrantha* (*K. gracilis*, *K. cristata*), *Calochortus venustus*, *Allium serratum*, *Lewisia rediviva*, *Astragalus gambellianus*, *Sanicula bipinnatifida*, and *Rigiopappus leptocladus*. Of the remaining taxa, more than half commonly or often grow on serpentine, but are by no means limited to it. Ten or fewer may be truly obligate serpentine plants. Perhaps there is here a difference of opinion as to the interpretation of the phrase "more obligate." However, the list does include species of rather widely differing ranges of tolerance with respect to the substratum and soils. Further observations on the relation of serpentine tolerant species to their substratum need to be stimulated.

Part I closes with a brief résumé of the history of botanical collecting in the area. Photographs of six collectors are presented. The annotated catalogue of vascular plants comprises Part II. Part III consists of a list of 34 general references and a glossary of technical terms. Part IV consists of an index of place names, an index of common names, and an index of scientific names.

The "Flora of the Santa Cruz Mountains of California" presents a synthesis of the present knowledge of the flora of the Santa Cruz Mountain area based on many collections by others as well as by Dr. Thomas. It represents a great deal of work and is a worthy volume which does credit to its author and will be useful to many. In conclusion, we will all, I am sure, concur wholeheartedly with the author's wish

that, by acquainting more people with the plants around them, this volume will serve as "a stimulus, however slight, toward more permanent protection of our environment."—MARY L. BOWERMAN, Department of Botany, University of California, Berkeley, California.

Principles of Plant Breeding. By R. W. ALLARD. xi + 485 pp. John Wiley & Sons, Inc. New York and London. 1960. \$9.00.

In the Preface, the author states that "Principles of Plant Breeding" is designed primarily to serve as an undergraduate text for students in agriculture. The aim of the book is to stress principles, and to illustrate them with appropriate examples. This task has been accomplished with a high degree of competence. Allard writes with clarity, precision and force. For this reason it should not be difficult for an undergraduate with some training in biometry, and a semester course in genetics, to follow his closely reasoned explanations and interpretations. The entire book is arranged to serve as a text for a two-semester course, but it is conveniently segmented so it can be adapted to the needs of a one-semester or one-quarter course. In addition to its pedagogical function, this book can be studied with profit by the professional plant breeder. It will serve to broaden his outlook and invigorate his research.

The material used to illustrate the principles is slanted to some extent towards cereal and forage crops, but this is not unnatural. More thorough information about plant breeding techniques and procedures is available for this group of crops than for fruit, vegetable, fiber or ornamental crops. A few more examples could, however, have been drawn from cotton and possibly other crops.

As one could anticipate, knowing his interests, the author is particularly sure-footed and lucid in chapters concerned with quantitative genetics, population genetics, systems of mating and heterosis. But other sections, for example, "Breeding methods with cross-pollinated crops," "Breeding for disease resistance," and "Polyploidy," are also discussed with equal skill.

This reviewer can suggest only one feature that would perhaps increase the usefulness of the book. A set of carefully composed questions and problems at the end of each chapter might serve as a source of understanding and stimulation. This has been done to some extent by inserting questions in the legends of a few figures. More complete development of this aspect might add to the teaching value of the book.

The references are not copious, but adequate for the purpose. The book is notable for an unusually low incidence of typographical errors. A glossary of terms used in plant breeding and a good index add to its serviceability.

It has taken time for plant breeding to bridge the gap between art and science. "Principles of Plant Breeding" is likely to be marked as a significant milestone in establishing plant breeding as a full-fledged scientific discipline.—THOMAS W. WHITAKER, U. S. Horticultural Field Station, La Jolla, California.

NOTES AND NEWS

The Smithsonian Institution is reprinting Paul C. Standley's *Trees and Shrubs of Mexico*, Contr. U. S. National Herbarium, vol. 23, 1920-26, Parts 1 (pp. xviii + 1-169), 2 (xxxvii + 171-515), 3 (pp. xxviii + 517-848), and 5 (ii + 1313-1721), in 2 paper-bound volumes containing pts. 1-3 and pt. 5, respectively. The price of these 4 parts is \$20, postpaid. Part 4 (pp. xxxiv + 849-1312), which is available in the original 1924 edition published by the U. S. National Museum, will be enclosed free of charge. Orders should be accompanied by check and should be addressed to: Publications Distribution Section, Smithsonian Institution, Washington 25, D.C.

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